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Impact of illumination on plant Photosystem II at different temperatures

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The photochemical activity of photosystem II (PSII) illuminated at different temperatures (20-55°C) has been studied. The photochemical activity of PSII preparations incubated at different temperatures in the dark decreased sharply in the range of 40-55°C, and was relatively stable at temperatures 20-40°C. The photochemical activity of PSII decreased with relatively monotonous kinetics in preparations processed at different temperatures and exposed to light, but in the end, it was higher than the activity observed in samples incubated in the dark. The effects of glycerin and sucrose on the PSII inhibition due to the exposure to different temperatures in darkness, and after temperature-light treatment were studied. The photochemical activity of PSII was measured after the incubation of the samples in a solution containing 50% glycerol (volume) or 1 M sucrose for 5 minutes in the dark at a certain temperature or under high light intensity at the same temperature. The photochemical activity of the PSII complex was found to be partially preserved in samples incubated in a glycerin-containing solution, at high temperatures, in both dark and light. The addition of sucrose to the solution resulted in a higher degree of protection of the photochemical activity of PSII.

Keywords: *Photosystem II, temperature, light, inhibition*

Abbreviations:* *BBY *((Berthold, Babcock, Yocum) Thylakoid membrane fragments enriched with PSII),* ***Cyt*** b_{559} *(Cytochrome* b_{559}*),* ***PSII*** *(Photosystem II),* F_V (F_0) *(Variable (initial) fluorescence of chlorophyll),* Q_A, Q_B *(Plastoquinones, electron acceptors),* ***MES*** *(4-Morpholinye-ethane-sulfonic acid), organic buffer),* P_{680} *(Primary donor of the electron in PSII),* ***Pheo*** *(Pheophytin),* ***RC*** *(Reaction center),* Y_Z, Y_D *(Tyrozines, electron donors of P680)*

INTRODUCTION

Environmental factors such as drought, salinity, and high temperature as well as toxic organic and inorganic substances intruding the environment due to technogenic disasters affect metabolic processes in plants and retard their development, thereby creating a serious danger to the ecosystem, agriculture and the development of the whole society (Krupa and Baszynski, 1995; Raven et al., 1999; Bertels and Sunkar R., 2005; Hasanuzzaman et al., 2013). Different mechanisms are involved in the response of plants to each of the extreme factors. However, under natural conditions, several factors affect the plant simultaneously and depending on the physiological state of the plant, the factor type, the duration and strength of the factor, more complex patterns of the response may occur (Havaux, 1992; Murata et al., 2007; Takahashi and Murata, 2008). One of the main targets affected by extreme factors in the plants is the photosynthetic process providing energy and oxygen for living things. Therefore, the study of the mechanisms of the effects of environmental factors on the functional activity of photosynthetic membranes, which is important for clarifying the balance of life processes on Earth, has become one of the substantial problems of modern biology.

Of the photosynthetic complexes, photosystem II (PSII) is more sensitive to unfavorable physicochemical factors, and the effect of the above factors

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on the photosynthetic apparatus of plants is mostly determined by PSII (Murata et al., 2007). PSII of plants, algae, and prokaryotic cyanobacteria is composed of ~30 proteins including light-harvesting antenna proteins, and numerous cofactors. Some of these cofactors are involved in light absorption and electron transfer, thereby providing the realization of the PSII function. The photochemical core of PSII includes PsbA (D_1), PsbD (D_2), PsbB (CP47), PsbC (CP43) and Cyt b_{559} proteins, and redox cofactors such as chlorophyll dimer P_{680}, pheophytin (Pheo), plastoquinones Q_A and Q_B, and tyrosine residues Y_Z (D_1-Tyr^{161}) and Y_D (D_2-Tyr^{161}). The main function of this complex is to catalyze the oxidation of water. This function is due to the cooperative action of the components of the PSII photochemical core (P_{680}, Pheo, Q_A, Q_B), Y_Z, and the Mn_4CaO_5 cluster. PsbO,P,Q (PsbO,U,V in cyanobacteria) proteins form the lumen domain of the PSII complex and participate in the stabilization of the Mn_4CaO_5 cluster (Shen, 2015).

In the initial stage of the energy conversion, the electron is transferred from the excited chlorophyll molecule (P_{680}*) to pheophytin for ~3 ps and the unstable $P_{680}^{\bullet+}Pheo^{\bullet-}$ pair is formed. In the subsequent stage, the electron is transferred from $Pheo^{\bullet-}$ to plastoquinone (Q_A) for ~200 ps and from tyrosine Y_Z to $P_{680}^{\bullet+}$ for 20-260 ns (Feyziyev, 2019). The oxidized tyrosine ($Y_Z^{\bullet+}$) receives an electron from the Mn_4CaO_5 cluster, which is the inorganic core of the water oxidation center. In general, PSII acts as "water- plastoquinone oxidoreductase" and catalyses the oxidation of two water molecules, ultimately resulting in the release of molecular oxygen to the atmosphere and 4 protons to the lumen of thylakoids. (Muh and Zouni, 2011).

The paper presents an *in vitro* study of the simultaneous effects of two different factors - high temperature and light on the photochemical activity of plant PSII preparations.

MATERIALS AND METHODS

PSII membrane preparations (BBY particles) were used in the study (Berthold et al., 1981; Völker et al., 1985). The experiment was carried out in the medium containing 50 mM MES-NaOH (pH6.1), 20 mM NaCl, 3 mM $MgCl_2$, and other components (glycerine, sucrose) were added when needed. The PSII preparations were incubated at different temperatures (in the range of 20–55°C) for 5 min in the dark or at a light intensity of ~80 μmol photon $m^{-2}s^{-1}$. After the inhibitory incubation period, the sample was diluted 3 times with the cold buffer solution, and fluorescence was measured.

The concentration of chlorophyll was determined spectrophotometrically measuring the optical density of its 80% acetone extract at 645 and 663 nm (MacKinney, 1941). The intensity of initial, variable, and maximum fluorescence of PSII (F_0, F_V, and F_M, respectively) was measured in an optical spectrometer supported by phosphororscope. The intensity and wavelength of measuring (which excite the fluorescence) and actinic (which excite the charge separation) light were ~5 μmol photon $m^{-2}s^{-1}$, λ=490 nm, and ~10^3 μmol photon $m^{-2}s^{-1}$, λ>650 nm, respectively. The concentration of chlorophyll in samples was 15 μg/ml.

The measurements were made in 3-6 repetitions, average values and standard deviations were determined.

RESULTS

We evaluated the photochemical activity of the isolated PSII membranes by measuring variable chlorophyll fluorescence. According to the measurements, the F_V/F_M value for the isolated FSII membranes was ~ 0.75 (75%). Since the value and kinetics of variable fluorescence characterize the electrons transfer from P_{680} to plastoquinone (Q_A) in PSII, it is widely used to evaluate the photochemical reaction proceeding at the reaction center (Kalaji et al., 2017; Feyziyev, 2019).

The isolated PSII membrane fragments were exposed to different temperatures in the dark and light for 5 min, and then variable fluorescence was measured in these samples. Figure 1 shows the kinetic changes of fluorescence at different temperatures.

As seen in the figure, variable fluorescence of chlorophyll was higher at room temperature (20°C) in both dark- and light-incubated preparations with values a little lower for the light-incubated ones (Curves 1 and 1a). This suggests that short-term incubation at room temperature did not affect the photochemical activity of the PSII preparations and that

the insignificant decrease in variable fluorescence of chlorophyll observed in the illuminated samples was most likely due to slight photoinhibition of PSII.

An increase in temperature caused a decrease in the intensity of variable fluorescence of chlorophyll in the dark and under illumination. These effects of temperature and light are demonstrated in figure 1 (curves 2 and 2a) for 45°C. As shown in the figure the intensity of variable fluorescence in illuminated preparations was lower than in the dark-incubated samples.

A further increase in temperature was accompanied by a slightly different effect. Thus, measurements at 52°C showed that the dark-incubated samples almost completely lost their photochemical activity, while the intensity of variable fluorescence in the illuminated samples still remained high (curves 3 and 3a). This indicates that the illuminated PSII membrane fragments partially retain their photochemical activity. It is clear that both thermoinhibition and photoinhibition occur at this temperature. However, it is likely that there exists a mechanism that positively influences the intensity of variable fluorescence - the photochemical activity of PSII. It can be assumed that this mechanism is the photoactivation of the Mn cluster inactivated thermally (Bao and Burnap, 2016).

Figure 2 shows the temperature dependence of the photochemical activity of PSII membranes incubated in the dark and under illumination in the temperature range of 20-52.5°C. According to the figure, the photochemical activity of PSII defined as the F_V/F_M ratio decreases with increasing temperature, both in the dark- and light-treated samples at different temperatures. However, this inhibition occurred in different ways: in dark-incubated samples, a slight decrease in photochemical activity occurred when rising the temperature up to ~45°C and in the subsequent short temperature range, a sharp decrease in the PSII photochemical activity was observed.

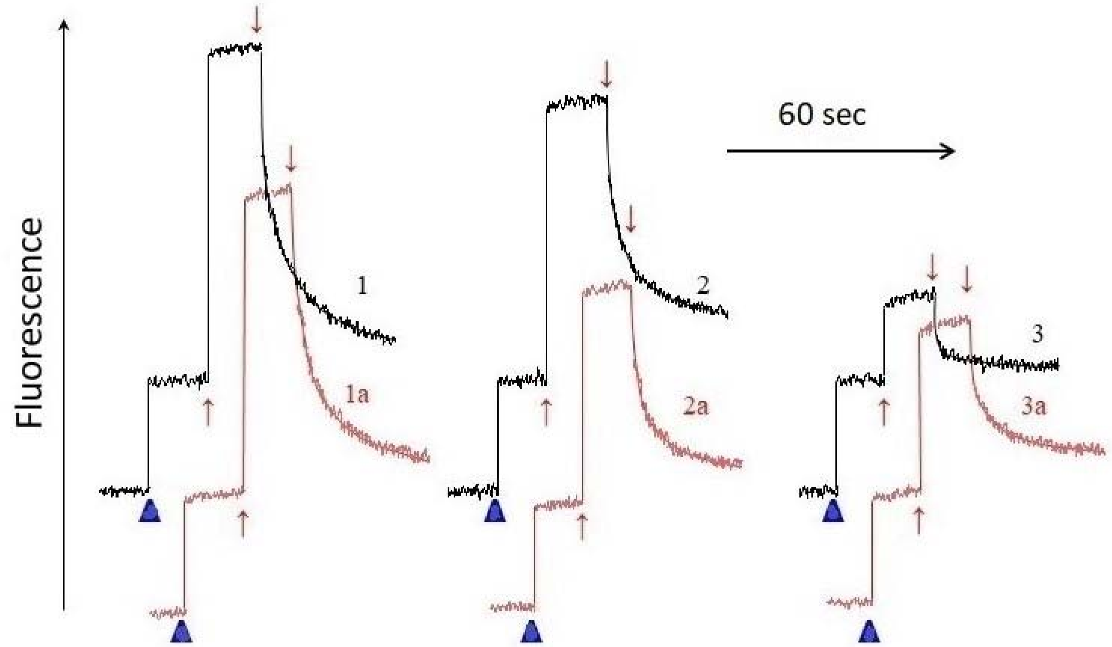


Fig. 1. Variable fluorescence of chlorophyll in PSII membrane fragments (BBY-particles) incubated at different temperatures in the dark and under illumination. PSII membrane fragments were incubated for 5 min at 20°C; 45°C and 52°C - in the dark (1, 2, and 3, respectively) or under illumination (1a, 2a, and 3a, respectively).
▲ – measuring light (490 nm; ~5μ mol photon $m^{-2}s^{-1}$) on; ↑ (↓) – actinic light (λ>650 nm; ~1000 μ mol photon $m^{-2}s^{-1}$) on (off).

Whereas, in the light-incubated samples, a monotonous decrease in PSII photochemical activity was detected with increasing temperature in the whole considered temperature range. Although in the temperature range of 20-35°C, its value was in the same order as that of the dark-incubated preparations, in the temperature range of 35-50°C, it was lower than the activity typical of dark-incubated samples. Finally, the photochemical activity of PSII in the illuminated preparations was significantly higher than in the dark-treated samples.

All three processes – thermal inhibition and photoinhibition, and photoactivation – can be assumed to occur simultaneously in PSII membranes illuminated in the temperature range of 20-55°C, and that contrary to the dark-treated samples, the photochemical activity inherent in illuminated samples is determined by the balance of these three processes. Heat-induced inhibition and photoinhibition of preparations play a leading role in this balance at temperatures > 40°C. However, at temperatures >50°C, illumination demonstrated a clear effect on the photochemical activity of PSII samples (Fig. 2, red symbols) and the activity increased due to contribution to the photoactivation process. At temperatures <40°C, all three processes can be assumed to be equally probable.

Thus, the inhibition that occurs at high temperatures as a result of lighting is partially eliminated. We have studied the effect of glycerin and sucrose on the heat-induced inhibition occurring in the dark and light. These compounds are known to protect biological molecules from damage and are used to ensure their stability. For example, in our research, high concentrations (0.3-0.4 M) of sucrose are used in the preparatory isolation process (conducted at a temperature of 4°C). The results of our study are shown in Figure 3A (glycerin) and 3B (sucrose). The amount of glycerin and sucrose in the incubation medium was 50% and 1.0 M, respectively.

As seen in Figure 3, a photochemical activity of PSII remained almost stable in the glycerin-containing medium in the temperature range of 20-45°C, both in the dark and light. A gradual decrease (20-25%) occurs only at >45°C (45-55°C) temperatures.

A similar pattern was observed in the sucrose-containing medium: in this case, the photochemical activity of PSII remained stable in the temperature range of 20–45°C both in the dark and light and decreased by ~ 15% at subsequent >45°C temperatures (Fig. 3B).

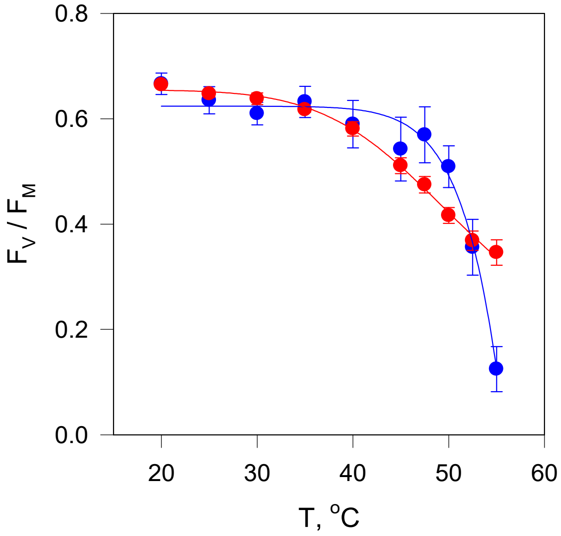


Figure 2. Temperature-dependent changes in the photochemical activity of the PSII preparations (BBY-particles) incubated at different temperatures in the dark and under illumination. The treatment of the samples at various temperatures in the dark (blue symbols) and under illumination (red symbols) was performed for 5 min. The light intensity was ~80 μmol photon $m^{-2}s^{-1}$. The experiments were conducted in the 50 mM MES-NaOH (pH 6.1) buffer solution containing 20 mM NaCl, 3 mM $MgCl_2$. The PSII membranes were incubated in the dark and light at various temperatures for 5 min and then diluted 3 times with the cold buffer solution and the measurements were made. The chlorophyll concentration was 15 μg/ml. The measurements were made in 3 repetitions, average values and standard deviations were calculated.

As seen in Figure 3, in both cases, the temperature factor plays a key role in inhibition, as the change in photochemical activity during lighting is almost indistinguishable from that observed in the dark-treated preparations. Thus, in these two cases, the roles of photoinhibition and photoactivation are not clear. It can be assumed that in both cases, the mechanism of heat-induced inhibition does not involve the electron transport of PSII on the donor side. For this reason, photoactivation of the catalytic center (Mn cluster and its immediate surroundings) where water is oxidized does not occur.

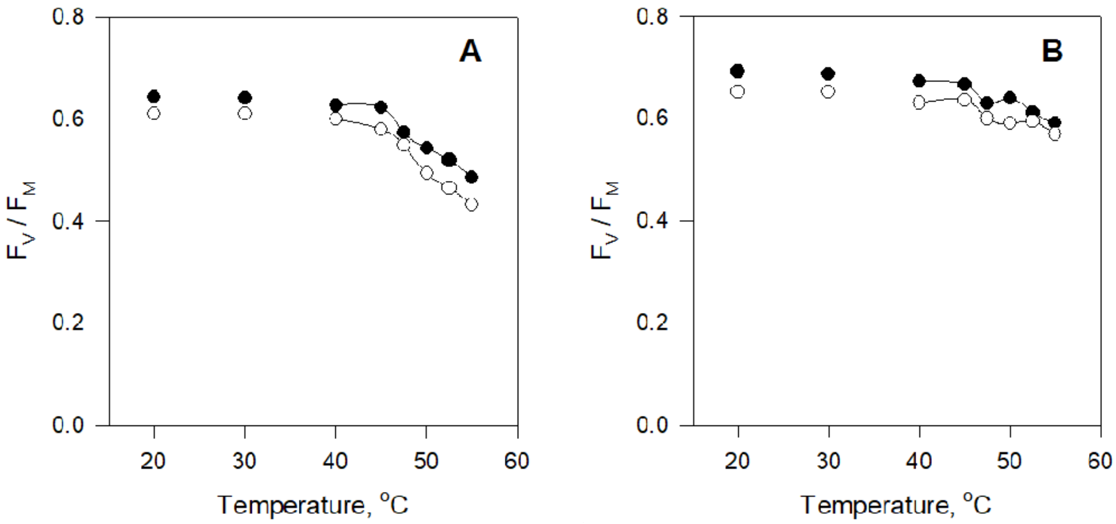


Figure 3. The effects of 50% (volume) glycerine (A) and 1M sucrose (B) on changes of photochemical activity of PSII at different temperatures in dark-incubated (black symbols) and light-incubated samples (light symbols). The measurements were made in 3 repetitions. Other parameters are shown in Fıgure 2.

Thus, the results of our research can be summarized as follows: (i) PSII complexes are inhibited both in the dark and light in the temperature range of 20°C–55°C. They gradually lose their photochemical activity with increasing temperature *in vitro*; (ii) The inhibitory effects of heat and lighting at high temperatures are not synergic: at temperatures >45°C, the thermal inhibition is partially eliminated by lighting; (iii) The compounds such as glycerin and sucrose prevent the inhibition of PSII preparations by both heat and the combined effects of heat and lighting.

DISCUSSION

The interesting aspects of PSII for researchers are related to the individual properties of this complex. Thus, first of all, PSII performs a very important biological function, such as the catalytic oxidation of water, and enriches the atmosphere with oxygen. The formation and existence of aerobic life on Earth are directly related to the activity of PSII. Second, this complex is the main target of many stress factors (heat, salinity, intense illumination, etc.), pollutants (heavy metals, organic compounds), and herbicides. This is attributed to the very fine structure of the PSII complex, the presence of high-affinity sites for organic and inorganic compounds. Third, in recent years, the creation of artificial devices based on the structure and function of biological complexes is in the focus of the alternative energy source projects. Along with other photosynthetic complexes, PSII may have a significant share in the realization of such concepts. Thus, the quantum yield of the initial photochemical reaction that takes place at its reaction center demonstrates a very high value (≥98%).-The primary electron donor of PSII in its oxidized form ($P_{680}^{\bullet+}$) has a very high (~ 1.2 V) potential that increases the interest for its practical usage. On the other hand, protons released to lumen as a result of the PSII activity, form an electrochemical gradient, besides ATP synthesis, they can be directed to the other metabolic processes (Feyziev, 2010; Barber and Tran, 2013; Maitra et al., 2014; Shen, 2015).

In all considered cases, the use of the properties of the PS II complex for practical purposes is limited due to its resistance to harmful effects of the environment, especially high temperatures, intense lighting, and pollutants. Given that these factors often coexist and act simultaneously, the combined effects of heat and light on PSII have been studied *in vitro*.

PSII is known to be inhibited under high temperatures as well as high light intensity (Yamashita et al., 2008; Yamomoto, 2001; 2016; Yin et al.,

2010). The inhibition depends on the duration of plant exposure to these factors. In our experiments, the exposure time was 5 min. This period is sufficient for the preparation to undergo heat shock *in vitro*. Changes in the PSII complex under the influence of heat are observed mainly at the biochemical level – proteins, lipids, enzymes, pigments, etc. As the incubation temperature of the preparation rises, a sharp decrease in the photochemical activity of the preparation, especially at high temperatures, occurs (Peters et al., 1999; Zhang et al., 2012).

In our experiments, the intensity of variable fluorescence decreased sharply starting from temperatures >45°C. This change under high temperatures may be primarily due to the loss of stability of the Mn cluster, as a result of perturbations on the donor side of PSII leading to dissociation of PsbO,P,Q proteins, and the elimination of this cluster from the binding site at very high temperatures (Bao and Burnap, 2015). Since such inactivation of the Mn cluster at very high temperatures is not reversible, the electron transport activity of the complex is completely inhibited.

Another mechanism of heat-induced inhibition occurs at the reaction center. This process is initiated by heat-induced damage to the lipid phase of the membrane or direct damage to RC proteins (Tsonev and Hirosaka, 2003). However, the role of these two mechanisms in the inhibition of photochemical activity (variable fluorescence) of PSII is not known, and these two processes can be assumed to occur with equal probability at high temperatures.

Several mechanisms can be involved in photoinhibition of PSII under high light intensity. These include extreme reduction of electron acceptor Q_A, the formation of a triplet ($^{T}P_{680}$ or $^{3}P_{680}$) or oxidized form of chlorophyll in RC ($P_{680}^{\bullet+}$), and inhibition of the PSII donor side. Photoinhibition can also occur in low-intensity lighting, and in this case, even the quantum yield of the process is expected to be higher.

However, in contrast to photoinhibition, which occurs in the PSII complex, there is also a positive photoactivation mechanism. This mechanism is always active in the process of *in vivo* assembly of the PSII complex, ensuring the reassembly of the water oxidation catalytic center during the *de nova* synthesis of proteins. In PSII complexes, which donor side is inhibited by the elimination of the Mn cluster *in vitro*, in addition to other factors, a photoactivation phase is required for the reassembly of the Mn cluster and restoration of electron transport (oxygen-evolving activity) (Bao and Burnap, 2015). Thus, in PSII, both inhibition and recovery processes can occur during illumination.

Our results can be explained by the above-mentioned mechanisms of heat-induced inhibition, photoinhibition, and photoactivation. Thus, in our experiments, the share of heat thermoinhibition and photoinhibition mechanisms in the general inhibition of electron transport is small on the donor side of PSII at temperatures ≤45°C. Therefore, the photoactivation effects are not visually observed in this temperature range. However, at temperatures > 45°C, the perturbation in the Mn cluster of PSII caused by temperature is likely to be eliminated by photoactivation during lighting. Thus, due to photoactivation, the complete thermal inhibition of the photochemical activity of PSII is prevented. However, in the end, photochemical activity (electron transport) does not fully recover under illumination. A simple explanation for this is the possibility of irreversible changes in the membrane structure and RC under high temperatures, as well as the activation of an inhibitory mechanism at the expense of $P_{680}^{\bullet+}$ during photoinhibition.

This scheme can explain the maintenance of physiological activity for a long time and the survival of plants under high temperature and light intensity. Thus, in this case, along with the antioxidant system, the photoactivation process is probably one of the main protection mechanisms.

The observed protective role of the compounds such as glycerin and sucrose against high temperature and combined effect of high temperature and lighting is a feature of each compound demonstrated against heat-induced inhibition as well as photoinhibition of the PSII complex. Thus, a slight inhibition of PSII occurs in the medium containing these compounds, therefore, there is almost no need for photoactivation, and this phenomenon is not observed.

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Müxtəlif temperaturlarda bitkilərin ikinci fotosisteminə işıqlanmanın təsiri

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Fotosistem II (FSII) kompleksinin fotokimyəvi aktivliyi müxtəlif temperaturlarda (20-50°C) işıqlandırılaraq öyrənilmişdir. Qaranlıqda, müxtəlif temperaturlarda inkubasiya olunmuş FSII membran fraqmentlərinin fotokimyəvi fəallığının 40-55°C intervalında kəskin azalması, aşağı temperaturlarda (20-40°C) isə nisbətən sabit olması müşahidə olunmuşdur. Müxtəlif temperaturlarda işlənilmiş və işığın təsirinə məruz qalmış nümunələrdə FSII-nin fotokimyəvi fəallığı nisbətən monoton kinetika ilə azalmış, lakin sonda qaranlıqda inkubasiya edilmiş nümunələrdə müşahidə olunan fəallıqdan yüksək olmuşdur. Qliserin və saxarozanın FSII-nin temperatur (qaranlıq) və birgə temperatur/işıqlanma inhibirləşməsinə təsiri də öyrənilmişdir. Bunun üçün FSII membran fraqmentləri 50% qliserin (həcm) və ya 1 M saxaroza əlavə edilmiş məhlulda 5 dəq müddətində müəyyən temperaturda qaranlıqda və ya həmin temperaturda işıqda inkubasiya edilmişdir. Qliserin əlavə edilmiş mühitdə yüksək temperaturlarda həm qaranlıqda, həm də işıqda inkubasiya edilmiş nümunələrdə FSII kompleksinin fotokimyəvi fəallığı qismən mühafizə olunmuşdur. Məhlula saxarozanın (1M) əlavə olunması isə FSII kompleksinin fotokimyəvi fəallığının qliserinə nisbətən daha yüksək dərəcədə mühafizə olunması ilə nəticələnmişdir.

Açar sözlər: *Fotosistem II, temperatur, işıq, inhibirləşmə*

Влияние освещения на фотосистему II растений при разных температурах

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Исследована фотохимическая активность фотосистемы II (ФСII) растений при разных температурах (20-50°C). В препаратах ФСII, инкубированных в темноте при разных температурах, наблюдалось резкое снижение фотохимической активности в диапазоне 40-55°C и относительная стабильность при температурах 20-40°C. Фотохимическая активность ФСII снижалась относительно монотонной кинетикой в препаратах, обработанных при разных температурах на свету, но в итоге была выше,

чем активность, наблюдаемая в образцах, инкубированных в темноте. Было изучено влияние глицерина и сахарозы на ингибирование ФСII, вызванного воздействием температуры (темнота) и совместного влияния температуры и света. Фотохимическую активность ФSII измеряли после инкубации мембранных фрагментов в растворе, содержащем 50% глицерина (объем) или 1 М сахарозы, в течение 5 минут в темноте при определенной температуре или на свету при той же температуре. Установлено, что фотохимическая активность ФСII частично сохраняется в образцах, инкубированных в глицеринсодержащем растворе при высоких температурах как в темноте, так и на свету. Добавление сахарозы (1М) к раствору приводило к более высокой степени защиты фотохимической активности ФСII.

Ключевые слова: *Фотосистема II, температура, свет, ингибирование*